Defaunation in the Anthropocene

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REVIEW

Defaunation in the Anthropocene

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We live amid a global wave of anthropogenically driven biodiversity loss: species and population extirpations and, critically, declines in local species abundance. Particularly, human impacts on animal biodiversity are an under-recognized form of global environmental change. Among terrestrial vertebrates, 322 species have become extinct since 1500, and populations of the remaining species show 25% average decline in abundance. Invertebrate patterns are equally dire: 67% of monitored populations show 45% mean abundance decline. Such animal declines will cascade onto ecosystem functioning and human well-being. Much remains unknown about this "Anthropocene defaunation"; these knowledge gaps hinder our capacity to predict and limit defaunation impacts. Clearly, however, defaunation is both a pervasive component of the planet's sixth mass extinction and also a major driver of global ecological change.

In the past 500 years, humans have triggered a wave of extinction, threat, and local population declines that may be comparable in both rate and magnitude with the five previous mass extinctions of Earth's history (*1*). Similar to other mass extinction events, the effects of this "sixth extinction wave" extend across taxonomic groups, but they are also selective, with some taxonomic groups and regions being particularly affected (*2*). Here, we review the patterns and consequences of contemporary anthropogenic impact on terrestrial animals. We aim to portray the scope and nature of declines of both species and abundance of individuals and examine the consequences of these declines. So profound is this problem that we have applied the term "defaunation" to describe it. This recent pulse of animal loss, hereafter referred to as the Anthropocene defaunation, is not only a conspicuous consequence of human impacts on the planet but also a primary driver of global environmental change in its own right. In comparison, we highlight the profound ecological impacts of the much more limited extinctions, predominantly of larger vertebrates, that occurred during the end of the last Ice Age. These extinctions altered ecosystem processes and disturbance regimes at continental scales, triggering cascades of extinction thought to still reverberate today (*3*, *4*).

The term defaunation, used to denote the loss of both species and populations of wildlife (*5*), as well as local declines in abundance of individuals, needs to be considered in the same sense as deforestation, a term that is now readily recognized and influential in focusing scientific and general public attention on biodiversity issues (*5*). However, although remote sensing technology provides rigorous quantitative information and compelling images of the magnitude, rapidity, and extent of patterns of deforestation, defaunation remains a largely cryptic phenomenon. It can occur even in large protected habitats (*6*), and yet, some animal species are able to persist in highly modified habitats, making it difficult to quantify without intensive surveys.

Analyses of the impacts of global biodiversity loss typically base their conclusions on data derived from species extinctions (*1*, *7*, *8*), and typically, evaluations of the effects of biodiversity loss draw heavily from small-scale manipulations of plants and small sedentary consumers (*9*). Both of these approaches likely underestimate the full impacts of biodiversity loss. Although species extinctions are of great evolutionary importance, declines in the number of individuals in local populations and changes in the composition of species in a community will generally cause greater immediate impacts on ecosystem function (*8*, *10*). Moreover, whereas the extinction of a species often proceeds slowly (*11*), abundance declines within populations to functionally extinct levels can occur rapidly (*2*, *12*). Actual extinction events are also hard to discern, and International Union for Conservation of Nature (IUCN) threat categories amalgamate symptoms of high risk, conflating declining population and small populations so that counts of threatened species do not necessarily translate into extinction risk, much less ecological impact (*13*). Although the magnitude and frequency of extinction events remain a potent way of communicating conservation issues, they are only a small part of the actual loss of biodiversity (*14*).

The Anthropocene defaunation process

Defaunation: A pervasive phenomenon

Of a conservatively estimated 5 million to 9 million animal species on the planet, we are likely losing ~11,000 to 58,000 species annually (*15*, *16*). However, this does not consider population extirpations and declines in animal abundance within populations.

Across vertebrates, 16 to 33% of all species are estimated to be globally threatened or endangered (*17*, *18*), and at least 322 vertebrate species have become extinct since 1500 (a date representative of onset of the recent wave of extinction; formal definition of the start of the Anthropocene is still being debated) (table S1) (*17*, *19*, *20*). From an abundance perspective, vertebrate data indicate a mean decline of 28% in number of individuals across species in the past four decades (fig. S1, A and B) (*14*, *21*, *22*), with populations of many iconic species such as elephant rapidly declining toward extinction (*19*).

Loss of invertebrate biodiversity has received much less attention, and data are extremely limited. However, data suggest that the rates of decline in numbers, species extinction, and range contraction among terrestrial invertebrates are at least as severe as among vertebrates (*23*, *24*). Although less than 1% of the 1.4 million described invertebrate species have been assessed for threat by the IUCN, of those assessed, ~40% are considered threatened (*17*, *23*, *24*). Similarly, IUCN data on the status of 203 insect species in five orders reveal vastly more species in decline than increasing (Fig. 1A). Likewise, for the invertebrates for which trends have been evaluated in Europe, there is a much higher proportion of species with numbers decreasing rather than increasing (*23*). Long-term distribution data on moths and four other insect orders in the UK show that a substantial proportion of species have experienced severe range declines in the past several decades (Fig. 1B) (*19*, *25*). Globally, long-term monitoring data on a sample of 452 invertebrate species indicate that there has been an overall decline in abundance of individuals since 1970 (Fig. 1C) (*19*). Focusing on just the Lepidoptera (butterflies and moths), for which the best data are available, there is strong evidence of declines in abundance globally (35% over 40 years) (Fig. 1C). Non-Lepidopteran invertebrates declined considerably more, indicating that estimates of decline of invertebrates based on Lepidoptera data alone are conservative (Fig. 1C) (*19*). Likewise, among pairs of disturbed and undisturbed sites globally, Lepidopteran species richness is on average 7.6 times higher in undisturbed than disturbed sites, and total abundance is 1.6 times greater (Fig. 1D) (*19*).

Patterns of defaunation

Although we are beginning to understand the patterns of species loss, we still have a limited understanding of how compositional changes in communities after defaunation and associated disturbance will affect phylogenetic community structure and phylogenetic diversity (*26*). Certain lineages appear to be particularly susceptible to human impact. For instance, among vertebrates, more amphibians (41%) are currently considered

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threatened than birds (17%), with mammals and reptiles experiencing intermediate threat levels (*27*).

Although defaunation is a global pattern, geographic distribution patterns are also decidedly nonrandom (*28*). In our evaluation of mammals (1437 species) and birds (4263 species), the number of species per 10,000 km^2 in decline (IUCN population status "decreasing") varied across regions from a few to 75 in mammals and 125 in birds (Fig. 2), with highest numbers in tropical regions. These trends persist even after factoring in the greater species diversity of the tropics (*29*, *30*). Similarly, most of 177 mammal species have lost more than 50% of their range (*9*).

The use of statistical models based on life history characteristics (traits) has gained traction as a way to understand patterns of biodiversity loss (*31*). For many vertebrates, and a few invertebrates, there has been excellent research examining the extent to which such characteristics correlate with threat status and extinction risk (*32*–*34*). For example, small geographic range size, low reproductive rates, large home range size, and large body size recur across many studies and diverse taxa as key predictors of extinction risk, at least among vertebrates. However, these "extinction models" have made little impact on conservation management, in part because trait correlations are often idiosyncratic and context-dependent (*31*).

We are increasingly aware that trait correlations are generally weaker at the population level than at the global scale (*31*, *35*). Similarly, we now recognize that extinction risk is often a synergistic function of both intrinsic species traits and the nature of threat (*32*, *34*–*37*). For example, large body size is more important for predicting risk in island birds than mainland birds (*34*) and for

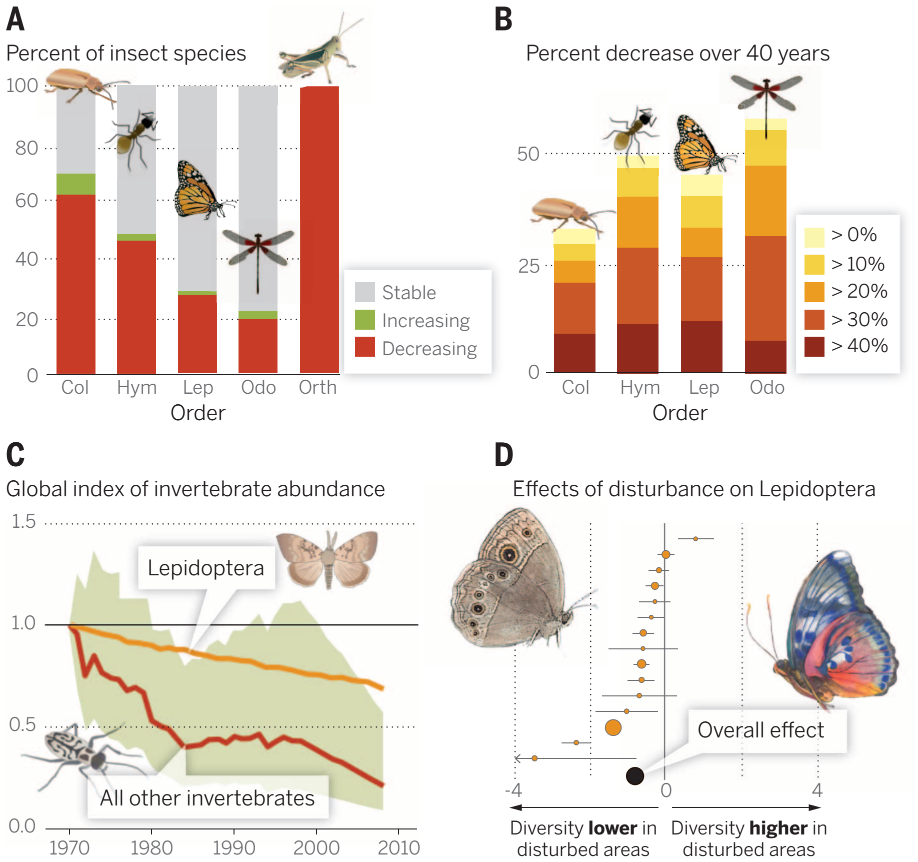


Fig. 1. Evidence of declines in invertebrate abundance. (**A**) Of all insects with IUCN-documented population trends, 33% are declining, with strong variation among orders (*19*). (**B**) Trends among UK insects (with colors indicating percent decrease over 40 years) show 30 to 60% of species per order have declining ranges (*19*). (**C**) Globally, a compiled index of all invertebrate population declines over the past 40 years shows an overall 45% decline, although decline for Lepidoptera is less severe than for other taxa (*19*). (**D**) A meta-analysis of effects of anthropogenic disturbance on Lepidoptera, the best-studied invertebrate taxon, shows considerable overall declines in diversity (*19*).

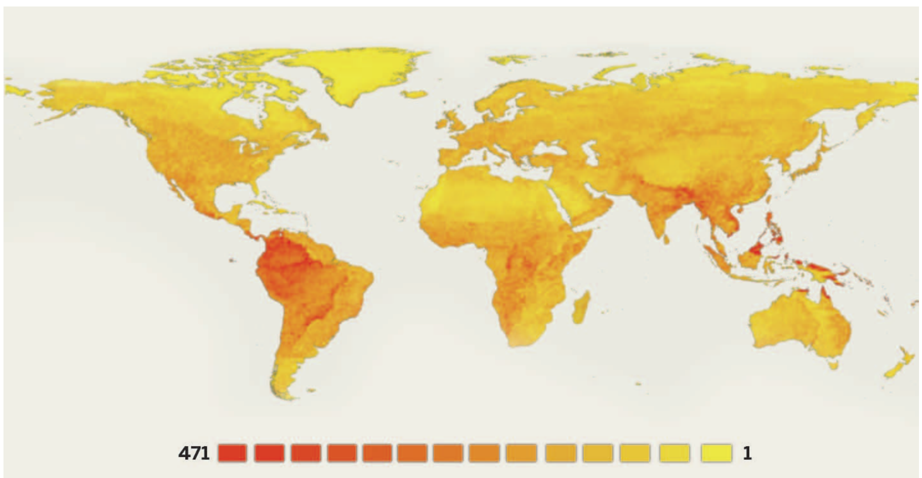


Fig. 2. Global population declines in mammals and birds. The number of species defined by IUCN as currently experiencing decline, represented in numbers of individuals per 10,000 km^2 for mammals and birds, shows profound impacts of defaunation across the globe.

tropical mammals than for temperate ones (*36*). However, increasingly sophisticated approaches help to predict which species are likely to be at risk and to map latent extinction risk (*38*), holding great promise both for managing defaunation and identifying likely patterns of ecological impact (*39*). For instance, large-bodied animals with large home ranges often play specific roles in connecting ecosystems and transferring energy between them (*40*). Similarly, species with life history characteristics that make them robust to disturbance may be particularly competent at carrying zoonotic disease and therefore especially important at driving disease emergence (*41*, *42*).

The relatively well-established pattern of correlation between body size and risk in mammals creates a predictable size-selective defaunation gradient (Fig. 3) (*19*, *36*, *43*). For instance, there are strong differences in body mass distributions among mammals that (i) became extinct in the Pleistocene [<50,000 years before the present (B.P.)], (ii) went recently extinct (<5000 years B.P., Late Holocene and Anthropocene), (iii) are currently threatened with extinction (IUCN category "threatened" and above), and (iv) extant species not currently threatened (Fig. 3), all showing greater vulnerability of larger-bodied species. The myriad consequences of such differential defaunation have been quantified via the experimental manipulation of the large wildlife in an African savanna (Fig. 4 and table S3), revealing substantial effects on biodiversity, ecological processes, and ecosystem functioning.

Multiple unaddressed drivers of defaunation

The long-established major proximate drivers of wildlife population decline and extinction in terrestrial ecosystems—namely, overexploitation, habitat destruction, and impacts from invasive species—remain pervasive (*18*). None of these major drivers have been effectively mitigated at the global scale (*14*, *18*). Rather, all show increasing trajectories in recent decades (*14*). Moreover, several newer threats have recently emerged, most notably anthropogenic climate disruption, which will likely soon compete with habitat loss as the most important driver of defaunation (*44*). For example, ~20% of the landbirds in the western hemisphere are predicted to go extinct because of climate change by 2100 (*45*). Disease, primarily involving human introduced pathogens, is also a major and growing threat (*46*).

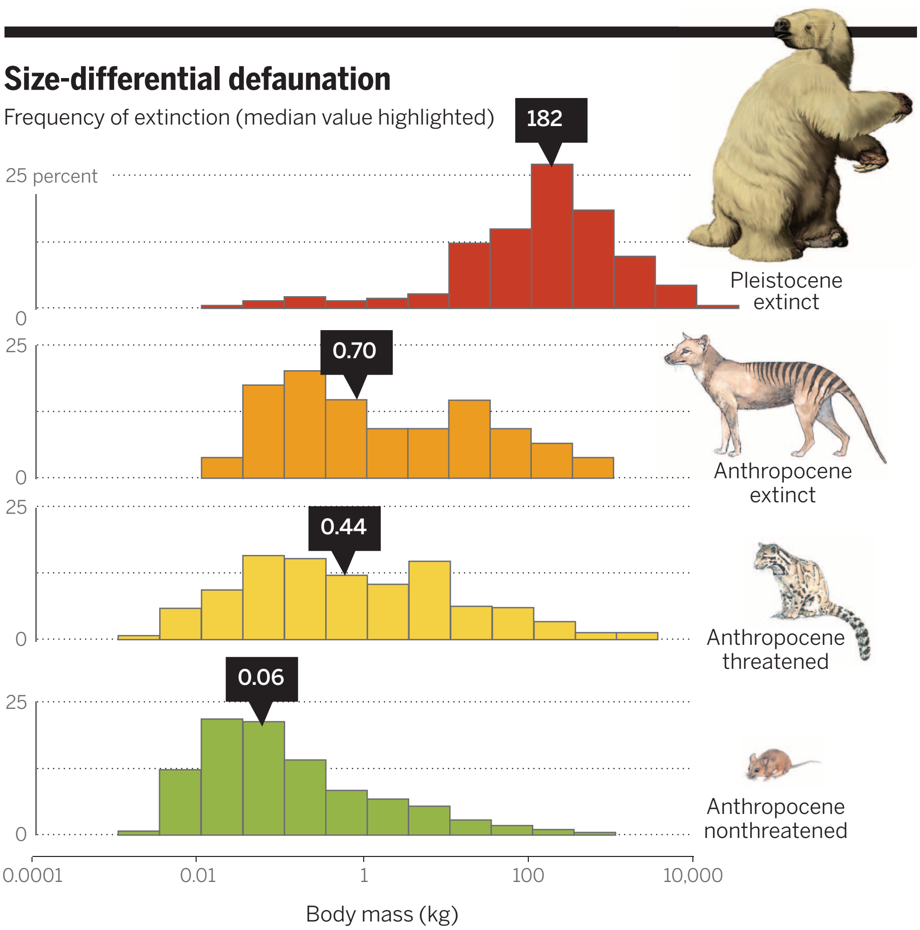


Fig. 3. Extinction and endangerment vary with body size. Comparing data on body size of all animals that are known to have gone extinct in Pleistocene or are recently extinct (<5000 years B.P.) shows selective impact on animals with larger body sizes (median values denoted with black arrow). Differences in body masses between distributions of currently threatened and nonthreatened species suggest ongoing patterns of size-differential defaunation (Kolmogorv-Smirnov test, $K = 1.3$, $P < 0.0001$) (*19*). [Animal image credits: giant sloth, C. Buell; others, D. Orr]

Although most declining species are affected by multiple stressors, we still have a poor understanding of the complex ways in which these drivers interact and of feedback loops that may exist (*7*, *11*). Several examples of interactions are already well documented. For example, fragmentation increases accessibility to humans, compounding threats of reduced habitat and exploitation (*47*). Similarly, land-use change is making it difficult for animals to expand their distributions into areas made suitable by climate change (*25*, *48*). Feedbacks among these and other drivers seem more likely to amplify the effects of defaunation than to dampen them (*11*).

Consequences of defaunation

Because animal loss represents a major change in biodiversity, it is likely to have important effects on ecosystem functioning. A recent meta-analyses of biodiversity-ecosystem function studies suggests that the impact of biodiversity losses on ecosystem functions is comparable in scale with that of other global changes (such as pollution and nutrient deposition) (*9*). However, most efforts to quantify this relationship have focused largely on effects of reduced producer diversity, which may typically have much lower functional impacts than does consumer loss (*49*, *50*). Efforts to quantify effects of changes in animal diversity on ecosystem function, particularly terrestrial vertebrate diversity, remain more limited (*19*, *51*).

Impacts on ecosystem functions and services

We examined several ecosystem functions and services for which the impacts of defaunation have been documented that are either a direct result of anthropogenic extirpation of service-providing animals or occur indirectly through cascading effects (Fig. 5).

Pollination

Insect pollination, needed for 75% of all the world's food crops, is estimated to be worth ~10% of the economic value of the world's entire food supply (*52*). Pollinators appear to be strongly declining globally in both abundance and diversity (*53*). Declines in insect pollinator diversity in Northern Europe in the past 30 years have, for example, been linked to strong declines in relative abundance of plant species reliant on those pollinators (*54*). Similarly, declines in bird pollinators in New Zealand led to strong pollen limitation, ultimately reducing seed production and population regeneration (Fig. 5H) (*55*).

Pest control

Observational and experimental studies show that declines in small vertebrates frequently lead to multitrophic cascades, affecting herbivore abundance, plant damage, and plant biomass (*56*).

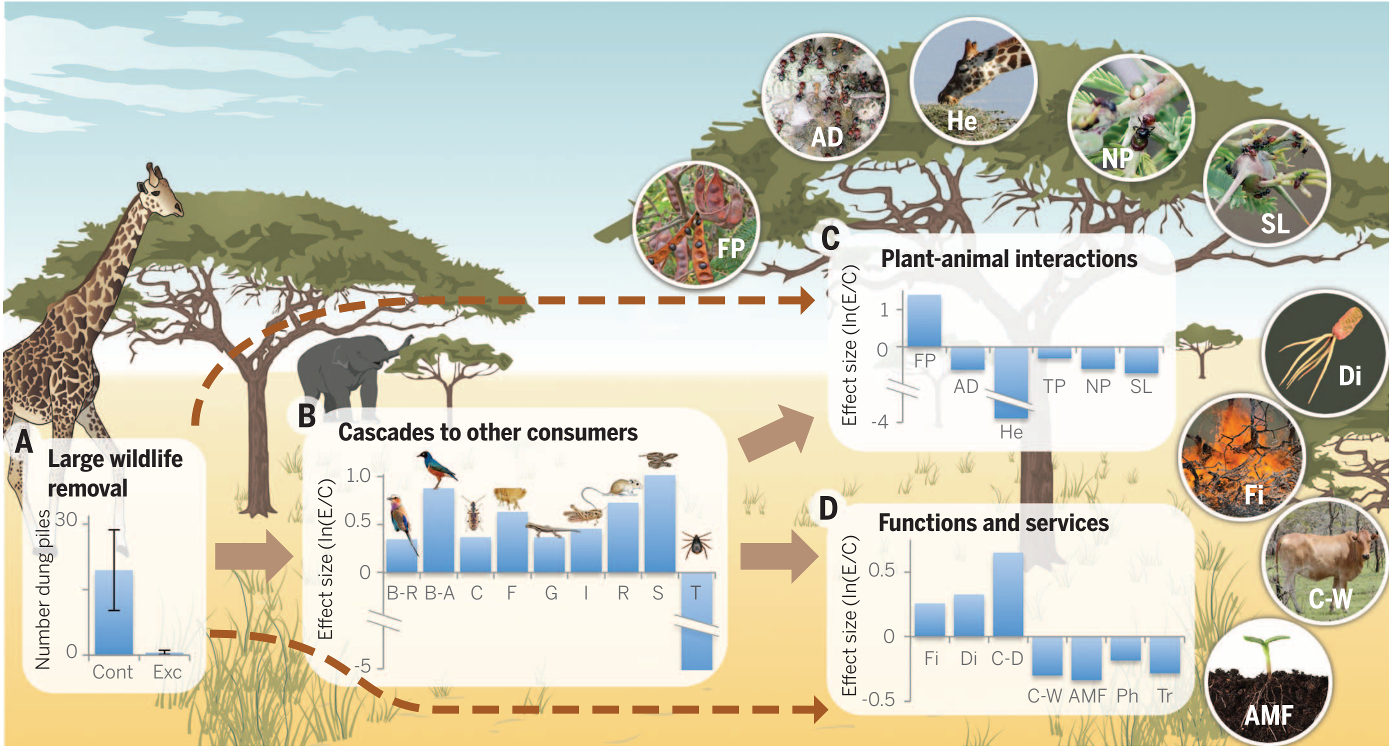


Fig. 4. Results of experimental manipulation simulating differential defaunation. As a model of the pervasive ecosystem effects of defaunation, in just one site (the Kenya Long Term Exclosure Experiment), the effects of selective large-wildlife (species >15 kg) removal drive strong cascading consequences on other taxa, on interactions, and on ecosystem services (*81*). (**A**) In this experiment, large wildlife are effectively removed by fences, as evidenced by mean difference in dung abundance (±1 SE) between control and exclosure plots. (**B**) This removal leads to changes in the abundance or diversity of other consumer groups. Effects were positive for most of these small-bodied consumers—including birds (B-R, bird species richness; B-A, granivorous bird abundance), Coleoptera (C), fleas (F), geckos (G), insect biomass (I), rodents (R), and snakes (S)—but negative for ticks (T). (**C**) Experimental defaunation also affects plant-animal interactions, notably altering the mutualism between ants and the dominant tree, *Acacia drepanolobium* and driving changes in fruit production (FP), ant defense by some species (AD), herbivory of shoots (He), thorn production (TP), nectary production (NP), and spine length (SL). (**D**) Large-wildlife removal also causes major effects on ecosystem functions and services, including changes to fire intensity (Fi), cattle production in both dry (C-D) and wet (C-W) seasons, disease prevalence (D), infectivity of arbuscular mycorrhizae fungi (AMF), photosynthetic rates (Ph), and transpiration rates (TR). Data in (B) to (D) are effect size [ln(exclosure metric/control metric)] after large-wildlife removal. Although this experiment includes multiple treatments, these results represent effects of full exclosure treatments; details on treatments and metrics are provided in table S3. [Photo credits: T. Palmer, H. Young, R. Sensenig, and L. Basson]

Cumulatively, these ubiquitous small-predator trophic cascades can have enormous impacts on a wide variety of ecological functions, including food production. For example, arthropod pests are responsible for 8 to 15% of the losses in most major food crops. Without natural biological control, this value could increase up to 37% (*57*). In the United States alone, the value of pest control by native predators is estimated at $4.5 billion annually (*58*).

Nutrient cycling and decomposition

The diversity of invertebrate communities, particularly their functional diversity, can have dramatic impacts on decomposition rates and nutrient cycling (*59*–*61*). Declines in mobile species that move nutrients long distances have been shown to greatly affect patterns of nutrient distribution and cycling (*62*). Among large animals, Pleistocene extinctions are thought to have changed influx of the major limiting nutrient, phosphorus, in the Amazon by ~98%, with implications persisting today (*3*).

Water quality

Defaunation can also affect water quality and dynamics of freshwater systems. For instance, global declines in amphibian populations increase algae and fine detritus biomass, reduce nitrogen uptake, and greatly reduce whole-stream respiration (Fig. 5E) (*63*). Large animals, including ungulates, hippos, and crocodiles, prevent formation of anoxic zones through agitation and affect water movement through trampling (*64*).

Human health

Defaunation will affect human health in many other ways via reductions in ecosystem goods and services (*65*), including pharmaceutical compounds, livestock species, biocontrol agents, food resources, and disease regulation. Between 23 and 36% of all birds, mammals, and amphibians used for food or medicine are now threatened with extinction (*14*). In many parts of the world, wild-animal food sources are a critical part of the diet, particularly for the poor. One recent study in Madagascar suggested that loss of wildlife as a food source will increase anemia by 30%, leading to increased mortality, morbidity, and learning difficulties (*66*). However, although some level of bushmeat extraction may be a sustainable service, current levels are clearly untenable (*67*); vertebrate populations used for food are estimated to have declined by at least 15% since 1970 (*14*). As previously detailed, food production may decline because of reduced pollination, seed dispersal, and insect predation. For example, loss of pest control from ongoing bat declines in North America are predicted to cause more than $22 billion in lost agricultural productivity (*68*). Defaunation can also affect disease transmission in myriad ways, including by changing the abundance, behavior, and competence of hosts (*69*). Several studies demonstrate increases in disease prevalence after defaunation (*41*, *42*, *70*). However, the impacts of defaunation on disease are far from straightforward (*71*), and few major human pathogens seem to fit the criteria that would make such a relationship pervasive (*71*). More work is

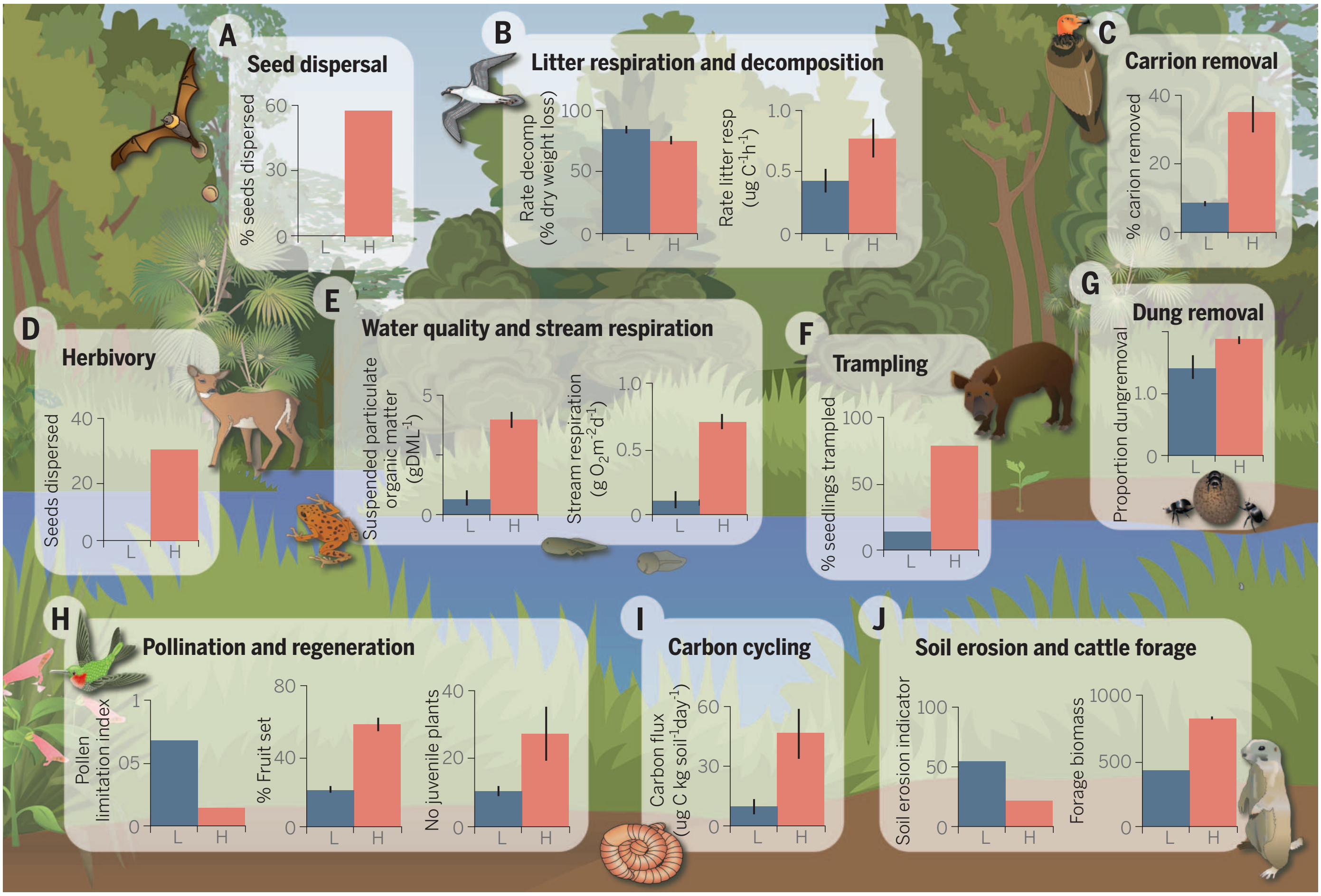


Fig. 5. Consequences of defaunation on ecosystem functioning and services. Changes in animal abundance from low (blue, L) to high (red, H) within a region have been shown to affect a wide range of ecological processes and services (*19*), including (**A**) seed dispersal (flying foxes), (**B**) litter respiration and decomposition (seabirds), (**C**) carrion removal (vultures), (**D**) herbivory (large mammals), (**E**) water quality and stream restoration (amphibians), (**F**) trampling of seedlings (mammals), (**G**) dung removal (dung beetles), (**H**) pollination and plant recruitment (birds), (**I**) carbon cycling (nematodes), and (**J**) soil erosion and cattle fodder (prairie dogs).

urgently needed to understand the mechanisms and context-dependence of defaunation-disease relationships in order to identify how defaunation will affect human disease.

Impacts on evolutionary patterns

The effects of defaunation appear not to be merely proximally important to the ecology of affected species and systems but also to have evolutionary consequences. Several studies have detected rapid evolutionary changes in morphology or life history of short-lived organisms (*72*) or human-exploited species (*73*). Because defaunation of vertebrates often selects on body size, and smaller individuals are often unable to replace fully the ecological services their larger counterparts provide, there is strong potential for cascading effects that result from changing body-size distributions (*74*). Still poorly studied are the indirect evolutionary effects of defaunation on other species, not directly affected by human defaunation. For example, changes in abundance or composition of pollinators or seed dispersers can cause rapid evolution in plant mating systems and seed morphology (*75*, *76*). There is a pressing need to understand the ubiquity and importance of such "evolutionary cascades" (*77*).

Synthesis and ways forward

This Review indicates that a widespread and pervasive defaunation crisis, with far-reaching consequences, is upon us. These consequences have been better recognized in the case of large mammals (*78*, *79*). Yet, defaunation is affecting smaller and less charismatic fauna in similar ways. Ongoing declines in populations of animals such as nematodes, beetles, or bats are considerably less evident to humans yet arguably are more functionally important. Improved monitoring and study of such taxa, particularly invertebrates, will be critical to advance our understanding of defaunation. Ironically, the cryptic nature of defaunation has strong potential to soon become very noncryptic, rivaling the impact of many other forms of global change in terms of loss of ecosystem services essential for human well-being.

Although extinction remains an important evolutionary impact on our planet and is a powerful social conservation motivator, we emphasize that defaunation is about much more than species loss. Indeed, the effects of defaunation will be much less about the loss of absolute diversity than about local shifts in species compositions and functional groups within a community (*80*). Focusing on changes in diversity metrics is thus unlikely to be effective for maintaining adequate ecological function, and we need to focus on predicting the systematic patterns of winners and losers in the Anthropocene and identify the traits that characterize them because this will provide information on the patterns and the links to function that we can then act on.

Cumulatively, systematic defaunation clearly threatens to fundamentally alter basic ecological functions and is contributing to push us toward global-scale "tipping points" from which we may not be able to return (*7*). Yet despite the dramatic rates of defaunation currently being observed, there is still much opportunity for action. We must more meaningfully address immediate drivers of defaunation: Mitigation of animal overexploitation and land-use change are two feasible, immediate actions that can be taken (*44*). These actions can also buy necessary time to address the other critical driver, anthropogenic climate disruption.

However, we must also address the often nonlinear impacts of continued human population growth and increasingly uneven per capita consumption, which ultimately drive all these threats (while still fostering poverty alleviation efforts). Ultimately, both reduced and more evenly distributed global resource consumption will be necessary to sustainably change ongoing trends in defaunation and, hopefully, eventually open the door to refaunation. If unchecked, Anthropocene defaunation will become not only a characteristic of the planet's sixth mass extinction, but also a driver of fundamental global transformations in ecosystem functioning.

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SUPPLEMENTARY MATERIALS

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REVIEW

Reversing defaunation: Restoring species in a changing world

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The rate of biodiversity loss is not slowing despite global commitments, and the depletion of animal species can reduce the stability of ecological communities. Despite this continued loss, some substantial progress in reversing defaunation is being achieved through the intentional movement of animals to restore populations. We review the full spectrum of conservation translocations, from reinforcement and reintroduction to controversial conservation introductions that seek to restore populations outside their indigenous range or to introduce ecological replacements for extinct forms. We place the popular, but misunderstood, concept of rewilding within this framework and consider the future role of new technical developments such as de-extinction.

Recent analyses have shown that the rate of biodiversity loss has not slowed despite global commitments made through the 2002 Convention on Biological Diversity (*1*). Projected future extinction rates for terrestrial species might exceed current rates of extinction (*2*). A key component of biodiversity loss is defaunation, the loss or depletion of animal species from ecological communities (*3*, *4*). Such losses can reduce the stability of